# NOTES ON THE ECOLOGY AND NATURAL HISTORY OF TWO UNCOMMON TERRESTRIAL AGAMID LIZARDS *CTENOPHORUS CLAYI* AND *C. FORDI* IN THE GREAT VICTORIA DESERT OF WESTERN AUSTRALIA

By ERIC R. PIANKA
Integrative Biology
University of Texas at Austin
Austin, Texas 78712 USA
Email: erp@austin.utexas.edu

## ABSTRACT

Ecological data on *Ctenophorus clayi* and *Ctenophorus fordi* are presented. *Ctenophorus clayi* is a habitat generalist found on sites close to sandridges, whereas *Ctenophorus fordi* is a terrestrial habitat specialist, typically found only on sites with sandridges with which it is closely associated, (habitat niche breadths = 3.7 and 2.13, respectively). Individuals are usually found either near spinifex tussocks or bushes or in the open. Microhabitat niche breadths are 4.1 and 2.99, respectively.

These lizards are active thermoregulators: Ambient air temperatures for *C. clayi* average 29.6°C and active body temperatures average 36.9°C. Ambient air temperatures for *C. fordi* average about 26.3°C and active body temperatures average 37.2°C. Average time of activity is during midday around 1100–1200 hrs.

Grasshoppers are the most important prey of *C. clayi* (30.5% by volume) which also consume termites (9.6%) and ants (9.5%) as well as hemipterans (7.6% by volume). Ants are the most important prey of *C. fordi* (45.7% by volume) which also consume hemipterans (14.0% by volume) and wasps (11.8% by volume) as well as smaller quantities of other insects. *C. clayi* has a broader dietary niche breadth than *C. fordi* which is an ant specialist. Dietary niche breadths are 6.35 and 3.96, respectively.

In both species, mating occurs during the Austral Spring, when eggs are laid. Clutch size in *C. clayi* varies from 1 to 4 and averages 2.77 eggs (N = 27). Clutch size in *C. fordi* is usually 2 eggs (mean = 2.3, N = 13). Relative clutch mass (RCM) of 24 gravid female *C. clayi* with oviductal eggs is 19.9% whereas RCM of one gravid female *C. fordi* with 2 eggs in her oviducts is 4.4%.

Aspects of the ecologies of these two terrestrial species are compared. Both *Ctenophorus clayi* and *C. fordi* are

uncommon and both are found only on study sites located near sandridges, but *C. clayi* has a much broader habitat niche as compared to *C. fordi*. Like two other arboreal sandridge agamid species *Diporiphora* and *Lophognathus* (Pianka 2013), both these terrestrial species exhibit features suggestive of metapopulation structure, such as dispersal propagules and/or being absent from sites with suitable habitats and microhabitats.

## INTRODUCTION

During Austral springs and summers of 1966–68, I encountered only one *Ctenophorus clayi* at a sandridge study site, the E-area (8 km NE Dunges Table Hill, 28° 08' S. x 123° 55' E.) in the Great Victoria Desert. In subsequent years, *C. clayi* was much more abundant at two other long-term nearby study sites (Redsands: 10 km WSW Yamarna, 28° 12' S. x 123° 35' E., and 4 km South of Redsands on the B-area: 140 km East of Laverton, 28° 13' 30" S. x 123° 35' 30" E.).

**Figure 1.** Adult *Ctenophorus clayi*.

During the same time period, the Austral Springs and summers of 1966–68, I encountered a population of *Ctenophorus fordi* at the same sandridge study site, the E-area (8 km NE Dunges Table Hill, 28° 08' S. x 123° 55' E.) in the Great Victoria Desert. In many years of subsequent field work at other sites, I never found any more populations of *C. fordi* but I did collect one lone adult gravid female at my sandplain G-area (27 km S Neale Junction, 28° 30' x 125° 50') and one lone male at my long-term Redsands study site (10 km WSW Yamarna, 28° 12' S. x

**Figure 2.** Adult female *Ctenophorus fordi*.

123° 35' E.). The G-area female can be considered a reproductive dispersal propagule, far away from sandridges making this species an example of a meta-population. Similarly, I witnessed extinction of the last lone male at Redsands (this individual could also be considered a failed dispersal propagule).

Neither species was encountered in apparently suitable sandridge habitats during extensive pit trapping from 2003 to 2006 at Lorna Glen, about 300+ km to the NW (Mark Cowan, pers. comm.).

Merely being in an alien habitat is not necessarily a death sentence, as these habitats offer shelter and food — a migrant that succeeds in reaching its correct habitat could also reap the benefits of sweepstakes reproductive success.

The Great Victoria Desert of Australia is predominantly sandy with red sands, and supports a vegetation consisting mainly of so-called "spinifex" or "porcupine" grasses (genus *Triodia*) plus various species of gum trees (*Eucalyptus*), especially Marble Gums (*Eucalyptus gonglyocarpa*) and various shrubs including *Eremophila*, *Grevillea*, *Hakea*, and *Thryptomene*. Stabilized long red sandridges, parallel to prevailing winds are scattered throughout the Great Victoria Desert, particularly in the eastern interior. Extensive areas of flat sandplain occur as well. The region is very heterogeneous with mixed ecotonal habitats of shrubs, *Triodia*, *Acacia*, and *Eucalyptus* on desert loams. Beard (1974) and Shephard (1995) describe and illustrate the vegetation of the region. The climate is an arid continental regime, with cool usually dry winters and warm springs and autumns but quite hot summers. Most precipitation falls during summer thunderstorms. Wildfires are frequently set by lightning and vegetation biomass and cover vary through time as plants undergo secondary sucession following fire (Pianka 1996; Pianka and Goodyear 2012).

## METHODS

My assistants and I observed and collected 293 *Ctenophorus clayi* at 3 study areas and nearby incidental non-study areas between 1966 and 2008. We observed and collected 110 *Ctenophorus fordi* on the E-area plus the singletons at two other study sites described above, as well as a few lizards on nearby incidental non-study areas. We recorded air and body temperatures, times of activity, microhabitat, fresh snout-vent length (SVL), tail length, and weight for as many lizards as possible. Stomach contents were identified and prey volumes estimated for all lizards collected. Reproductive condition was also recorded: for males, lengths of testes were measured; for females, egg sizes were measured and numbers counted, and whether eggs were ovarian or oviductal was noted [some of these data were summarized in appendices in Pianka (1986)]. Niche breadths were calculated using the inverse of Simpson's (1949) index of diversity [$D = 1/\ \Sigma p_i^{\ 2}$] where $p_i$ is the proportion of resource state *i*. Habitat niches are based on four dimensions, microhabitat niches on 15 dimensions, and dietary niches on 20 dimensions.

## RESULTS

### Habitat

Although *Ctenophorus clayi* is usually found on sites close to sandridges, it is a habitat generalist, with a broad habitat niche breadth. In contrast, *Ctenophorus fordi* is a habitat specialist with a much narrower habitat niche breadth, which strongly prefers slopes and crests of sandridges (Table 1).

**Table 1.** Numbers and percentages of lizards found in four different sandridge habitat zones. Lizards at an interface between habitats are split between shared habitats. Sample size (N), habitat niche breadths (HNB), and standardized HNBs, standardized by division by 4 are given at bottom of the table.

| **Habitat** | ***C. clayi*** | | ***C. fordi*** | |
|---|---|---|---|---|
| **Number, %** | N | % | N | % |
| **Flat** | 59 | 27.3 | 1 | 0.9 |
| **Base** | 64.5 | 29.9 | 3 | 2.6 |
| **Slope** | 27.5 | 12.7 | 60 | 52.6 |
| **Crest** | 65 | 30.1 | 50 | 43.9 |
| **Sample (N)** | **216** | | **114** | |
| **HNB** | **3.7** | | **2.13** | |
| **Standardized HNB** | **0.925** | | **0.533** | |

### Microhabitat

*Ctenophorus clayi* is often found in the open sun, but is also associated with spinifex tussocks and less often with bushes (Table 2). Three lizards were slightly above ground when first sighted. *Ctenophorus fordi* is also a microhabitat specialist, usually found either in the open sun or associated with large bushes.

### Thermoregulation

Body temperatures of 40 active *Ctenophorus clayi* ranged from 30.3 to 42.8°C averaging 36.9°C with a standard deviation of 2.67 (average air temperature was 29.6°C with a standard deviation of 4.25). Body temperature is weakly correlated with air temperature (Figure 3).

*Ctenophorus fordi* is also an active thermoregulator. Body temper-

**Table 2.** Percentages of lizards encountered in 9 different microhabitats. Microhabitat niche breadths (MHNB) are given at the bottom of the table.

| | ***Ctenophorus clayi*** | | ***Ctenophorus fordi*** | |
|---|---|---|---|---|
| **Microhabitat** | **N** | **%** | **N** | **%** |
| Open Sun | 18.5 | 37 | 56.5 | 50.9 |
| Grass Sun | 14.25 | 28.5 | 4 | 3.6 |
| Bush Sun | 3.25 | 6.5 | 17.5 | 15.8 |
| Other Sun | 0 | 0 | 1 | 0.9 |
| Open Shade | 3.5 | 7 | 4 | 3.6 |
| Grass Shade | 5.25 | 10.5 | 3 | 2.7 |
| Bush Shade | 2.25 | 4.5 | 24 | 21.6 |
| Other Shade | 0 | 0 | 1 | 0.9 |
| Low Sun | 3 | 6 | 0 | 0 |
| Sample (N) | 50 | | 111 | |
| **MHNB** | **4.1** | | **2.99** | |

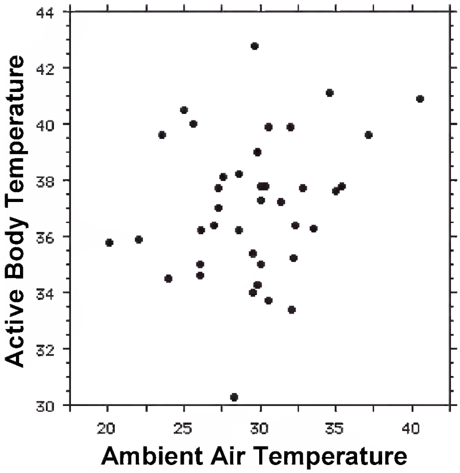


**Figure 3.** Body temperatures plotted against ambient air temperatures for 40 active *C. clayi.*

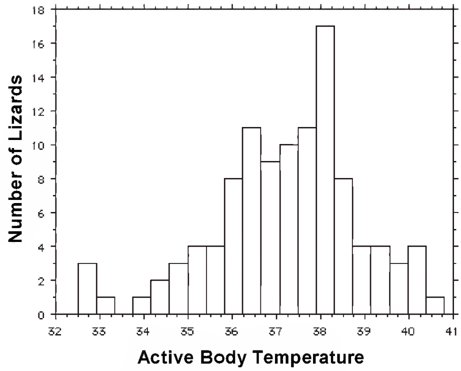


**Figure 4.** Histogram of active body temperatures in *C. fordi.*

atures of 108 active lizards ranged from 32.5 to 40.8°C averaging 37.2°C with a standard deviation of 1.65 (Figure 4) Average air temperature was 26.3°C with a standard deviation of 4.73. Body temperature is significantly correlated (r = 0.52, P < 0.01) with air temperature (Figure 5).

Like most heliothermic diurnal desert lizards, both of these species bask when it is cold, and seek shade or go down into burrows when it is hot. During

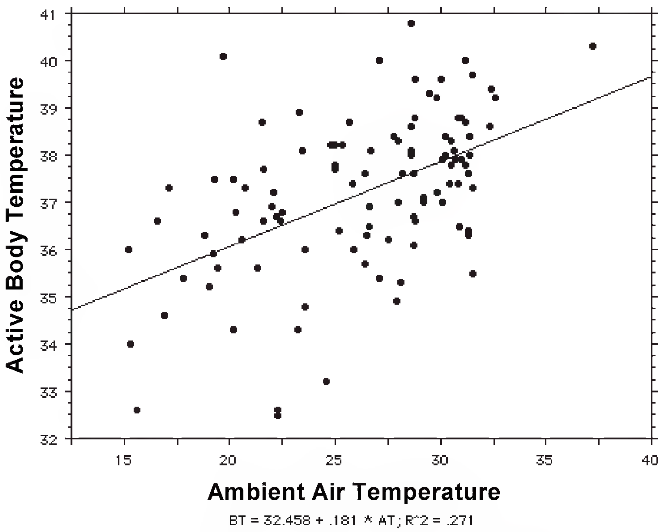


**Figure 5.** Active body temperatures plotted against ambient air temperature for 108 active *C. fordi.*

the heat of mid-day, *C. clayi* sometimes climb up above ground and face directly into the sun, thereby positioning themselves in cooler air and reducing heat load. Climbing also increases the area of their visual field and presumably may help them avoid contact with potential predators.

## Diets

Both species are sit-and-wait ambush predators. *C. clayi* has a fairly broad diet (Dietary niche breadth = 6.35, Table 3). Grasshoppers are the most important insect prey item eaten (30.5% of diet by volume). Termites and ants constitute 9.6 and 9.5% of the diet by volume, respectively. Hemipterans, scorpions, beetles, spiders, and wasps are eaten in smaller amounts. Ants are the most important insect prey item eaten (45.7%) by *C. fordi*. Hemipterans (14.0% of diet by volume) and wasps (11.8% of diet by volume) are also eaten. Grasshoppers constitute 5.1% of the diet by volume (Table 3). Dietary niche breadth of *C. fordi* is moderate at 3.96.

## Reproduction

As judged by enlarged testes in male *C. clayi* and females carrying eggs, both sexes reach maturity at about the same size, around 44–45 mm in SVL. *C. clayi* females were gravid from October through February (N=27).

**Table 3.** Composition of the diets of two terrestrial species of *Ctenophorus*.

| | *Ctenophorus clayi* | | | *Ctenophorus fordi* | | |
|---|---|---|---|---|---|---|
| | No. | Vol. | % | No. | Vol. | % |
| Centipedes | 9 | 0.22 | 0.77 | 1 | 0.1 | 0.75 |
| Spiders | 61 | 1.19 | 4.20 | 24 | 0.65 | 4.86 |
| Scorpions | 2 | 2.1 | 7.36 | 2 | 0.01 | 0.07 |
| Ants | 516 | 2.71 | 9.49 | 2031 | 6.12 | 45.74 |
| Wasps | 44 | 0.96 | 3.36 | 56 | 1.58 | 11.81 |
| Locustids | 122 | 8.7 | 30.47 | 18 | 0.68 | 5.08 |
| Thysanurans | 54 | 0.59 | 2.07 | 7 | 0.13 | 0.97 |
| Roaches | 6 | 0.12 | 0.42 | 0 | 0 | 0.00 |
| Mantids/ Phasmids | 5 | 0.2 | 0.70 | 0 | 0 | 0.00 |
| Beetles | 65 | 2.08 | 7.29 | 37 | 0.38 | 2.84 |
| Termites | 0 | 2.73 | 9.56 | 2 | 0.02 | 0.15 |
| Hemipterans | 117 | 2.16 | 7.57 | 212 | 1.87 | 13.98 |
| Diptera | 5 | 0.11 | 0.39 | 8 | 0.27 | 2.02 |
| Lepidoptera | 0 | | | 4 | 0.26 | 1.94 |
| Larvae | 29 | 1.07 | 3.75 | 4 | 0.35 | 2.62 |
| Other Insects | 12 | 0.53 | 1.86 | 27 | 0.71 | 5.31 |
| Vegetation | 13 | 0.39 | 1.37 | 13 | 0.25 | 1.87 |
| Other Unidentified | 91 | 2.68 | 9.39 | 3 | 0 | 0 |
| **Totals** | **1151** | **28.54** | **100.0** | **2445** | **13.38** | **100** |
| **Dietary N. B.** | | | **6.35** | | | **3.96** |

Average clutch size is 2.77. Relative clutch mass (clutch weight as a percentage of female body weight) is 19.9%. *C. clayi* hatchlings are small (SVL 23–27 mm). Juveniles grow fast and probably suffer fairly heavy mortality.

30 adult male *C. fordi* with enlarged testes found from September to December averaged 50.7 mm in SVL. Average adult *C. fordi* female SVL is 51.3 mm. Clutch sizes of 13 female *C. fordi* were either 2 or 3 and averaged 2.3. Gravid females were found in September, October, November and early December. One gravid female *C. fordi* found in October contained 2 shelled eggs in her oviducts. Relative clutch mass of this one female *C. fordi* is 4.4%. Hatchlings emerge in early December and are small (SVL 25 mm).

Juvenile *C. fordi* grow fast and undoubtedly suffer fairly heavy mortality.

### Predation

Predators on both *C. clayi* and *C. fordi* include various species of birds of prey especially Brown Falcons and Australian Kestrels, bustards, large snakes, and the monitor lizards *Varanus eremius*, *Varanus tristis* and *Varanus gouldii* as well as introduced cats and foxes. Both species rely heavily on camouflage to avoid predators, typically freezing and holding very still until the threat goes away. However, if pursued, they run rapidly away from an attacker or dart down a burrow.

## DISCUSSION

### Comparisons

Both *Ctenophorus clayi* and *C. fordi* are uncommon and limited to only a few study sites with sandridges located nearby. However, whereas *C. clayi* is a habitat generalist found out on flats, base, slopes, and crests of sandridges, *C. fordi* is a specialist, closely restricted to slopes and crests of sandridges where 96.5% of lizards were found (two lone isolated individual *C. fordi* were found on areas G and R). *C. clayi* has a much broader habitat niche (3.7) as compared to *C. fordi* (only 2.13). Like two other arboreal sandridge agamid species *Diporiphora* and *Lophognathus* (Pianka 2013), both species exhibit features suggestive of metapopulation structure (Levins

**Table 4.** Presence/absence and sample sizes of 4 agamid species on 5 study sites.

| Species | D Sandridges | E Sandridges | G Sandplain | R Sandridges | B Sandplain (ridges nearby) |
|---|---|---|---|---|---|
| *Diporiphora* | 18 | 17 | | | |
| *Lophognathus* | 29 | 11 | | 40 | 2 juveniles |
| *C. clayi* | | 1 juvenile | | 234 | 45 |
| *C.fordi* | | 105 | 1 gravid ♀ | 1 adult ♂ | |

1969; Harrison et al. 1988), such as dispersal propagules, local extinctions, and/or being absent from sites with suitable habitats and microhabitats (Table 4).

Their use of microhabitats differs with 39% *C. clayi* found in spinifex sun or shade as compared to only 6.3% of *C. fordi*, which species is more often associated with sun or shade in the open or near bushes 88.3% as compared to only 55% in *C. clayi*. *C. clayi* has a broader microhabitat niche breadth (4.1) than *C. fordi* (2.99). Major prey of *C. clayi* is grasshoppers (30.5%), which constitute only 5.1% of the diet by volume in *C. fordi*, which in turn consume many more ants (45.7%) than *C. clayi* (only 9.5%). *C. fordi* eat 14.0% hemiptera and 11.8% wasps, as compared to only 7.6% and 3.4% respectively in *C. clayi*. *C. clayi* eat more termites (9.6%) and beetles (7.3%) than *C. fordi* (0.2%) and (2.8%), respectively. *C. clayi* has a broader dietary niche breadth (6.35) than *C. fordi* (3.96) which is an ant specialist.

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